

## Influence of agricultural landscape structure on a Southern High Plains, USA, amphibian assemblage

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### Abstract

Landscape structure can influence demographics of spatially structured populations, particularly less vagile organisms such as amphibians. We examined the influence of agricultural landscape structure on community composition and relative abundance of the 4 most common amphibians in the Southern High Plains of central USA. Amphibian populations were monitored using pitfall traps and drift fence at 16 playa wetlands (8 playas/year) in 1999 and 2000. We quantified landscape structure surrounding each playa via estimating 13 spatial metrics that indexed playa isolation and inter-playa landscape complexity. Multivariate ordination and univariate correlations and regressions indicated that landscape structure was associated with community composition and relative abundance for 2 of the 4 amphibians. Spadefoots (*Spea multiplicata*, *S. bombifrons*) generally were positively associated with decreasing inter-playa distance and increasing inter-playa landscape complexity. Great Plains toads (*Bufo cognatus*) and barred tiger salamanders (*Ambystoma tigrinum mavortium*) usually were negatively associated with spadefoots but not influenced by landscape structure. Composition and relative abundance patterns were related to amphibian body size, which can influence species vagility and perception to landscape permeability. Spatial separation of these species in the multivariate ordination also may have been a consequence of differential competitive ability among species. These results suggest agricultural landscape structure may influence abundance and composition of spatially structured amphibian populations. This also is the first applied documentation that inter-patch landscape complexity can affect intra-patch community composition of amphibians as predicted by metapopulation theory. In the Southern High Plains, landscape complexity is positively associated with agricultural cultivation. Agricultural cultivation increases sedimentation, decreases hydroperiod, alters amphibian community dynamics, and negatively impacts postmetamorphic body size of amphibians in playa wetlands. Thus, conservation efforts should focus on preserving or restoring native landscape structure, hydroperiod, and connectivity among playas to maintain native amphibian populations and historic inter-playa movement.

### Introduction

Landscape structure can influence demographics of spatially structured populations via influencing inter-demic movement (Fahrig and Paloheimo 1988). Components of landscape structure include spatial

positioning of habitat patches and the geometric matrix in which habitat patches are embedded (Fahrig and Merriam 1994). Relative abundance of wildlife generally declines as habitat patches become isolated (Lefkovitch and Fahrig 1985; Burel 1989). Moreover, as landscapes become more geometrically complex, probability of successful dispersal among habitat patches may decrease because inter-patch boundary

density increases (Stamps et al. 1987; Wiens 1997). Consequently, isolated populations embedded in complex landscapes may have a greater probability of extinction than those more optimally positioned within simpler landscapes (Fahrig and Merriam 1985; Taylor et al. 1993).

Most amphibian populations in temperate North America are spatially structured, because they exist in fragmented or naturally discontinuous wetlands. The relative abundance of amphibians has often been negatively correlated with habitat isolation in temperate and tropical climates (Marsh and Pearman 1997; Pope et al. 2000; Scribner et al. 2001). Agricultural cultivation between wetlands may intensify this effect by decreasing the inter-patch native vegetation (Marsh and Trenham 2001). Moreover, cultivation may affect community composition of amphibians by increasing inter-patch landscape complexity (e.g., edge density), which can affect probability of inter-demic movement as predicted by metapopulation theory (Wiens 1997). This effect may be more pronounced in prairie landscapes, such as the Southern High Plains, where natural edges were not historically abundant (Smith 2003).

Amphibians in the semi-arid Southern High Plains exist primarily in spatially structured playa wetlands (Smith 2003). There are approximately 20,000 individual playas in the Southern High Plains, and they represent the lowest topographic points on the relatively flat landscape (Guthery and Bryant 1982). Playas are generally circular in shape and their watersheds are not interconnected (Luo et al. 1997). Inter-playa distance and playa size vary greatly in the Southern High Plains (Smith and Haukos 2002). Primary land uses surrounding playas are agricultural cultivation and native or replanted grasslands. Due to differences in spatial patterns of anthropogenic land use in the Southern High Plains, inter-playa geometric complexity varies, with complexity increasing in agricultural landscapes (Gray 2002).

Because amphibians can interact among playas via dispersal (Gray 2002), landscape structure (i.e., playa spatial positioning and inter-playa landscape complexity) may be an important factor influencing local amphibian communities. No applied studies exist that have examined the effect of inter-patch landscape complexity on community composition of amphibians. Playa hydroperiod also is interrelated with landscape complexity in the Southern High Plains, because cultivated landscapes tend to be more geometrically complex. Agricultural cultivation de-

creases playa hydroperiod through increased sedimentation (Luo et al. 1999), which can affect reproductive potential and aquatic competition of amphibians in playas (Gray et al. 2004). Therefore, our goal was to determine the general influence of landscape structure on community composition and relative abundance of the 4 most common amphibians (*Spea multiplicata* Cope [New Mexico spadefoot], *S. bombifrons* Cope [plains spadefoot], *Bufo cognatus* Say [Great Plains toad], *Ambystoma tigrinum mavortium* Green [barred tiger salamander]) in the semi-arid Southern High Plains during 1999 and 2000. Understanding the influence of agricultural landscape structure on wildlife communities is important, particularly for assemblages in decline such as amphibians (Houlahan et al. 2000; Marsh and Trenham 2001; Guerry and Hunter 2002).

## Methods

Our study was conducted at 16 playa wetlands in the Southern High Plains, central USA. All playas had 25% of their circumference enclosed with a 60-cm high continuous drift fence (Dodd and Scott 1994). The drift fence was placed immediately adjacent to the playa edge at all study playas to ensure that capture of emerging amphibians was similar among playas. Pitfall traps (19-L) were placed every 10 m along the fences. Pitfalls were checked every day for captures from 16 May–17 October 1999 and 19 April–18 August 2000. Captured amphibians were enumerated by species, marked uniquely, and released. Age classes were pooled per species because capture data were insufficient to provide meaningful age-specific analyses. We used mean daily capture per species per playa as an estimate of species-specific relative abundance (Heyer et al. 1994). Sampling techniques followed approved Texas Tech University Animal Use and Care Committee protocol (permit #99843).

We quantified landscape structure surrounding each study playa using remote sensing from aerial photos and geographical information system and spatial analysis software. Landscapes ( $n = 16$ ) were 2,830-ha circular plots (i.e., 3-km radius) with their origins positioned at the center of each study playa (Gray 2002:177–180). We chose a 3-km radius to delineate the landscape plot, because this distance probably was the near maximum dispersal distance for our species (cf. Gehlbach 1967, Gehlbach et al. 1969; Sinsch 1990, 1997; Maud et al. 2000). Aerial images

of landscapes in summers 1999 and 2000 were obtained from the Farm Service Agency of the U.S. Department of Agriculture in Crosby, Floyd, Hale, and Castro counties, Texas. Ground control points were identified on images and U.S. Geological Survey 7.5-minute quadrangle maps then geo-corrected using ERDAS<sup>®</sup> software. Geo-referenced images were mosaicked in ERDAS<sup>®</sup> and cover types (i.e., crop type, replanted Conservation Reserve Program grass, or native grass) were identified in each landscape plot using 1999 and 2000 Farm Service Agency farm folders. Boundaries of cover types were digitized in ERDAS<sup>®</sup> then exported as an ESRI<sup>®</sup> ARC/INFO coverage. Coverages were cleaned, built, and polygons classified as per cover types in ESRI<sup>®</sup> ARC/INFO. Landscape structure was quantified per plot using FRAGSTATS\*ARC<sup>®</sup> (McGarigal and Marks 1995); we used the following 13 spatial metrics. Shape index of the study playa (PSI), study playa surface area (PS), mean nearest-neighbor distance from the study playa to surrounding playas (PNN), mean nearest-neighbor distance from all playas to each other (MNN), number of playas (NP), percent aerial coverage of playas (PP), and an interspersion/juxtaposition index of playas (IJI) were used to quantify relative spatial positioning and isolation of playa wetlands (McGarigal and Marks 1995). Mean number of edges to cross from the study playa to surrounding playas (PED), edge density (m edge/ha, ED), landscape shape index (i.e., measure of geometric complexity, LSI), land-use (i.e., cover type) richness (LR), Shannon evenness index of land uses (SEI), and Shannon diversity index of land uses (SDI) were used as measures relative landscape complexity (McGarigal and Marks 1995). These metrics were selected based on their potential to influence abundance and community composition of amphibians (McGarigal and Marks 1995; Rosenzweig 1995). Unity was assigned to cover types and edge permeabilities in FRAGSTATS\*ARC<sup>®</sup> (McGarigal and Marks 1995), because relative vagilities for our species were unknown.

Canonical correspondence analysis (CCA) was used to examine the influence of landscape structure metrics on relative abundance of species in the amphibian assemblage (ter Braak 1986, 1994). Correlated metrics ( $P \leq 0.05$ ) were removed prior to CCA to reduce probability of an arch effect (ter Braak 1995:139). Because CCA is sensitive to outliers and bimodally distributed data, relative abundance per species was natural-log transformed prior to analysis

(ter Braak 1995); all resulting distributions were unimodal with  $\leq 2$  outliers. A global Monte Carlo permutation test was performed to test for existence of a relationship between landscape metrics and species composition (ter Braak and Šmilauer 1998:47–49, 124–125). A dimensionless species-landscape metric biplot was constructed using CANOCO<sup>®</sup> to graphically examine the pattern of variation in relative species abundance with landscape metrics (ter Braak 1995; ter Braak and Šmilauer 1998). Biplot axes were interpreted by examining the sign and magnitude of their respective intra-set correlations and using subject-matter knowledge (ter Braak 1995:140). Length of metric-specific eigenvectors (i.e., the arrows) in the biplot was interpreted as the strength of correlation between the metric and species abundance (ter Braak 1995:141–142). Therefore, long eigenvectors were most important in affecting the species assemblage (ter Braak 1995:141). Relative correlative ranking of species with respect to the metrics was graphically represented by extending each eigenvector through the origin of the biplot and intersecting it with orthogonal lines drawn from the species (ter Braak 1995:143). Species positioned near the arrow- and blunt-end of the eigenvector were most positively and negatively correlated with the metric, respectively (ter Braak 1995:141–143).

Canonical correspondence analysis in CANOCO<sup>®</sup> does not provide univariate measures of association between individual metrics and species-specific abundance (ter Braak and Šmilauer 1998). Thus, we also calculated Pearson coefficients of correlation and tested for a linear relationship between each metric and species-specific abundance (Milton and Arnold 1995:425–430). Metrics that were correlated ( $P \leq 0.05$ ) with species-specific abundance also were regressed linearly using least-squares estimation, and univariate prediction models developed (Milton and Arnold 1995:386–391). Relative abundance per species was natural-log transformed for all correlation and regression analyses to satisfy ( $P > 0.05$  as per Shapiro-Wilk test) linear model assumptions (Milton and Arnold 1995:391–392).

## Results

Summary statistics of mean daily relative abundance per species per playa are presented (Table 1). Six of the 13 landscape metrics (PNN, NP, PED, ED, LSI, and SDI) were not used in the canonical correspon-

**Table 1.** Mean daily relative abundance of New Mexico spadefoot (NSF), plains spadefoot (PSF), Great Plains toad (GPT), and barred tiger salamander (BTS) at 16 playa wetlands in the Southern High Plains, Texas, 1999 and 2000.

Playa <sup>a</sup>	Species							
	NSF		PSF		GPT		BTS	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1	44.67	9.94	2.21	0.57	17.79	6.13	21.02	4.82
2	260.90	214.80	0.79	0.48	4.31	1.47	14.57	11.36
3	47.74	13.84	2.41	0.66	2.66	0.44	3.59	0.92
4	288.10	97.15	3.02	1.06	7.88	2.47	10.71	5.82
5	24.49	7.15	2.64	0.71	15.12	3.06	10.62	3.39
6	1.78	0.56	0.32	0.09	1.41	0.23	19.41	7.44
7	6.37	1.84	2.51	0.69	11.05	3.53	17.54	4.71
8	1.77	0.78	0.68	0.24	3.89	1.13	14.63	3.26
9	13.38	4.13	3.98	1.43	1.36	0.49	3.51	1.01
10	35.23	9.33	10.98	2.84	5.85	1.14	3.15	1.08
11	39.15	9.73	7.26	2.97	5.52	1.95	8.06	2.01
12	17.25	4.27	1.09	0.47	0.49	0.15	1.11	0.44
13	1.37	0.31	0.15	0.08	0.52	0.18	0.79	0.31
14	1.77	0.33	0.62	0.19	1.42	0.36	12.35	9.55
15	28.62	15.24	1.23	0.25	7.79	1.34	5.29	2.54
16	5.17	1.27	1.15	0.42	8.79	1.69	11.69	3.36

<sup>a</sup>Playas 1–4 and 9–12 were located in geometrically complex cultivated landscapes; whereas, playas 5–8 and 13–16 were located in geometrically simplistic grassland landscapes.

dence analysis, because they were correlated with other metrics (Gray 2002:64–65). The global Monte Carlo permutation test based on 199 permutations revealed that composition of the amphibian assemblage was associated ( $F = 2.201$ ,  $P = 0.049$ ) with landscape metrics. The first two canonical axes were most important in explaining variation in the amphibian assemblage (i.e., as per respective eigenvalues,  $\lambda_1 = 0.061$ ,  $\lambda_2 = 0.022$ ,  $\lambda_3 = 0.001$ ,  $\lambda_4 = 0.013$ ); they collectively explained 67.9% of variation in relative abundance. Intra-set correlations suggested that axes 1 and 2 explained variation in species abundance with respect to playa positioning and inter-playa landscape complexity, respectively, because of the large absolute magnitude of percent aerial playa coverage and juxtaposition for axis 1 and Shannon evenness index of land uses for axis 2 (Table 2). The dimensionless species-environmental biplot of axes 1 (ordinate) and 2 (abscissa) suggested that Shannon evenness index was most positively correlated (as per eigenvector length) with the pattern of species abundance (Figure 1a). Playa surface area, percent playa coverage, juxtaposition, and land-use richness were moderately correlated, and the shape index of the study playa and

**Table 2.** Intra-set correlations of landscape<sup>a</sup> metrics associated with the first two axes generated by a canonical correspondence analysis of relative abundance of New Mexico spadefoot, plains spadefoot, barred tiger salamander, and Great Plains toad at 16 playa wetlands in the Southern High Plains, Texas, 1999 and 2000.

Metric <sup>b</sup>	Correlations <sup>c</sup>	
	Axis 1	Axis 2
PSI	0.0202	− 0.1854
PP	− 0.6970	0.1859
IJI	− 0.7625	− 0.0788
MNN	0.1489	− 0.0134
LR	− 0.5559	− 0.2485
SEI	0.0092	− 0.7729
PS	− 0.3993	0.4379

<sup>a</sup>Landscapes ( $n = 16$ ) were 2830-ha circular plots (i.e., 3-km radius) with their origins positioned at the center of each study playa;

<sup>b</sup>PSI = shape index of study playa, PP = percent aerial coverage of playas, IJI = interspersal/juxtaposition index of playas, MNN = mean nearest-neighbor distance from all playas to each other, LR = land-use type richness, SEI = Shannon evenness index of land uses, and PS = study playa size (McGarigal and Marks 1995);

<sup>c</sup>Intra-set correlations are standardized and dimensionless thus they can be interpreted as the strength and direction of metric-specific correlation and species abundance in the presence of all other metrics (ter Braak 1995:140); we inferred that axes 1 and 2 explained variation in species abundance with respect to wetland positioning and landscape complexity because of the large absolute magnitude of PP and IJI for axis 1 and SEI for axis 2.

mean nearest neighbor distance least correlated with species composition patterns. Orthogonal inferred ranking of species against eigenvectors indicated that both spadefoot species were most positively associated with playa surface area, percent playa coverage, juxtaposition, and land-use richness; Great Plains toad and barred tiger salamander generally were negatively associated with these spatial metrics (Figure 1b). In contrast, Great Plains toad and barred tiger salamander were most positively, and spadefoot species most negatively, related with mean nearest neighbor distance of playas. Plains spadefoot also was negatively associated with Shannon evenness and playa shape indices (Figure 1b).

Relative abundance was correlated linearly with percent aerial playa coverage, juxtaposition, edge density, landscape shape index, mean number of edges between study playas, and land-use richness for New Mexico spadefoot and the first 4 aforementioned metrics for plains spadefoot; significant correlations were not detected for Great Plains toad or barred tiger salamander (Table 3). Approximately 26%, 27%, 45%, 47%, 48%, and 53% of the variation in relative abundance of New Mexico spadefoots was explained

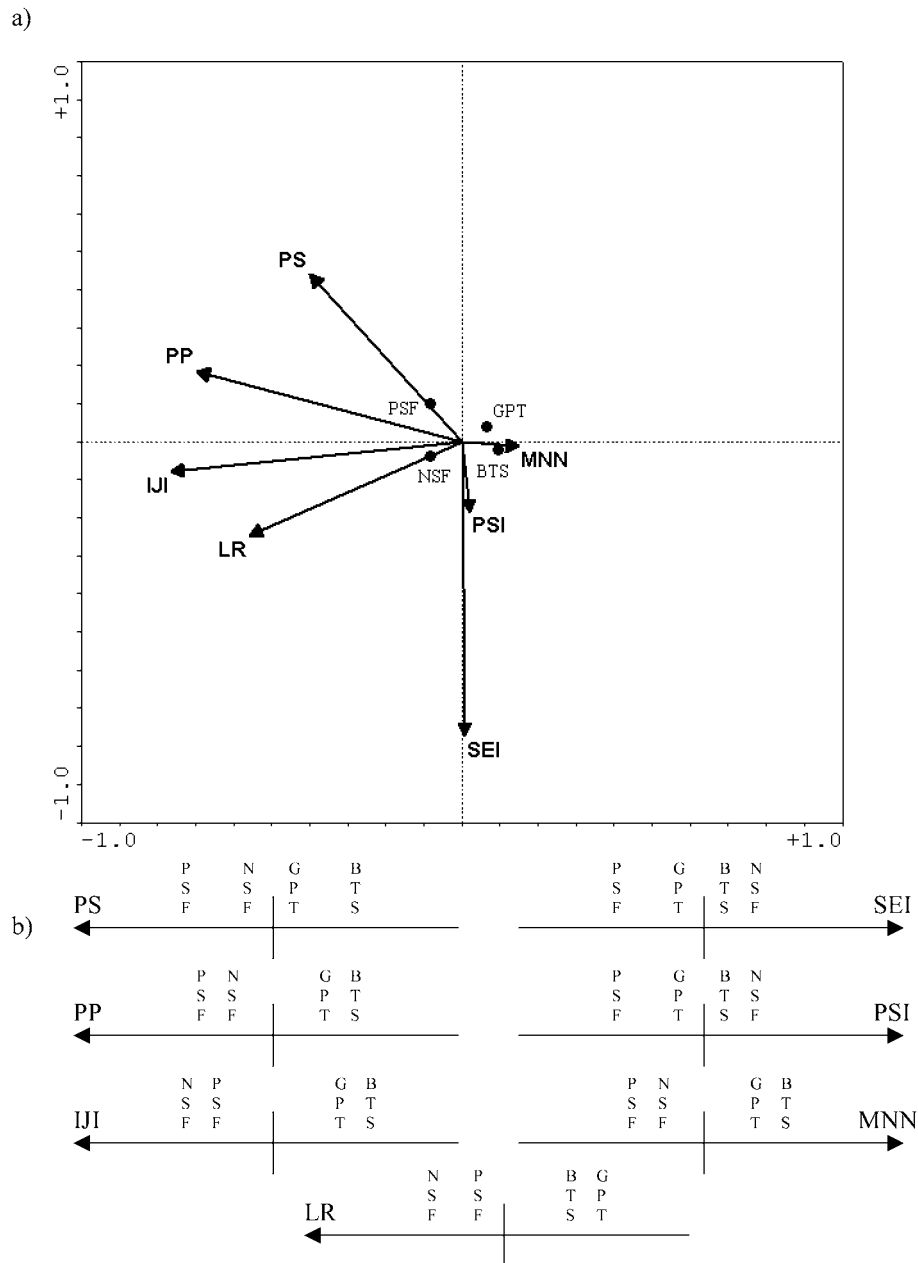


Figure 1. Canonical correspondence analysis of relative abundance (natural-log transformed) of amphibians and uncorrelated metrics in landscapes (i.e., 2,830-ha circular plot) associated with 16 study playas in the Southern High Plains, Texas, 1999 and 2000. (a) Species-environmental (i.e., – landscape metric) biplot (ter Braak 1995:142); axes 1 (ordinate) and 2 (abscissa) are dimensionless and represent wetland positioning and landscape complexity, respectively (see corresponding intra-set correlations in Table 1); length of eigenvectors (i.e., their respective eigenvalue) indicates the strength of correlation between the variable and pattern of variation in species composition (ter Braak 1995:141); species more close to ends of eigenvectors are more positively correlated with it; PS = study playa size, SEI = Shannon evenness index of land uses, PP = percent aerial coverage of playas, PSI = shape index of study playa, MNN = mean nearest-neighbor distance from all playas to each other, IJI = interspersed and juxtaposition index of playas, and LR = land-use richness (McGarigal and Marks 1995). (b) Inferred ranking of species along variables based on biplot interpretation of Part a of Figure (ter Braak 1995:143); ranking constructed by extending eigenvectors through the origin and intersecting with orthogonal lines from the species to the vector; the vertical segment represents the origin (i.e., centroid) of the biplot and is the grand mean of each variable; species more close to the arrow or blunt end are positively or negatively correlated with the variable, respectively. NSF = New Mexico spadefoot, PSF = plains spadefoot, GPT = Great Plains toad, and BTS = barred tiger salamander.



Table 3. Univariate Pearson coefficients of correlation between relative abundance of amphibians and landscape<sup>a</sup> metrics at 16 playa wetlands in the Southern High Plains, Texas, 1999 and 2000.

Variable <sup>b</sup>	Species <sup>c</sup>							
	NSF		PSF		BTS		GPT	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
PSI	−0.138	0.612	−0.175	0.515	−0.102	0.708	−0.284	0.286
PS	−0.011	0.970	0.274	0.304	−0.477	0.062	−0.138	0.611
PNN	−0.199	0.459	−0.284	0.287	0.102	0.708	−0.166	0.538
MNN	−0.405	0.119	−0.299	0.259	−0.322	0.224	−0.414	0.111
NP	0.432	0.095	0.388	0.138	−0.023	0.933	0.082	0.763
PP	0.506	0.046	0.592	0.016	−0.352	0.182	−0.073	0.787
IJI	0.726	0.002	0.589	0.016	−0.036	0.896	0.063	0.816
PED	0.518	0.039	0.457	0.075	−0.353	0.180	−0.186	0.492
ED	0.694	0.003	0.548	0.028	−0.234	0.383	0.048	0.858
LSI	0.687	0.003	0.571	0.021	−0.256	0.338	0.046	0.863
LR	0.670	0.005	0.249	0.351	−0.085	0.754	0.247	0.356
SEI	0.219	0.414	−0.473	0.065	0.104	0.701	−0.077	0.777
SDI	0.421	0.105	−0.297	0.263	0.055	0.838	0.032	0.905

<sup>a</sup>Landscapes ( $n = 16$ ) were 2830-ha circular plots (i.e., 3-km radius) with their origins positioned at the center of each study playa;

<sup>b</sup>PSI = shape index of study playa, PS = study playa size, PNN = mean nearest-neighbor distance from study playa to surrounding playas, MNN = mean nearest-neighbor distance from all playas to each other, NP = number of playas, PP = percent aerial coverage of playas, IJI = interspersal/juxtaposition index of playas, PED = mean number of edges to cross from study playa to surrounding playas, ED = edge density (m edge/ha), LSI = landscape shape index (i.e., measure of geometric complexity), LR = land-use type richness, SEI = Shannon evenness index of land uses, and SDI = Shannon diversity index of land uses (McGarigal and Marks 1995);

<sup>c</sup>NSF = New Mexico spadefoot, PSF = plains spadefoot, BTS = barred tiger salamander, and GPT = Great Plains toad.

by percent aerial playa coverage ( $F_{1,14} = 4.82$ ,  $P = 0.046$ ), mean number of edges between study playas ( $F_{1,14} = 5.14$ ,  $P = 0.04$ ), land-use richness ( $F_{1,14} = 11.41$ ,  $P = 0.005$ ), landscape shape index ( $F_{1,14} = 12.49$ ,  $P = 0.003$ ), edge density ( $F_{1,14} = 13.04$ ,  $P = 0.003$ ), and juxtaposition ( $F_{1,14} = 15.6$ ,  $P = 0.001$ ), respectively (Figure 2). Approximately 30%, 33%, 35%, and 35% of the variation in relative abundance of plains spadefoots was explained by edge density ( $F_{1,14} = 6.03$ ,  $P = 0.028$ ), landscape shape index ( $F_{1,14} = 6.78$ ,  $P = 0.021$ ), juxtaposition ( $F_{1,14} = 7.46$ ,  $P = 0.016$ ), and percent aerial coverage of playas ( $F_{1,14} = 7.55$ ,  $P = 0.016$ ), respectively (Figure 3).

## Discussion

Canonical correspondence analysis revealed that landscape structure influenced composition of this Southern High Plains amphibian assemblage. Landscape complexity between playa wetlands was most important in affecting species composition patterns, followed by playa positioning. Univariate analyses indicated New Mexico and plains spadefoots generally were positively associated with spatial metrics

representing optimal spatial positioning of playas (i.e., decreasing inter-playa distance) and agricultural landscape complexity (e.g., edge density) between playas. Great Plains toad and barred tiger salamander usually were negatively associated with spadefoots, but their relative abundance was not influenced by landscape structure.

Spadefoots may have been associated with landscape structure more than the other species in the assemblage because of their relatively small body size (Gray 2002). Body size has been shown to connote vagility (Peters 1983:89–91; With and Crist 1995), seemingly due to differential perception to inter-habitat patch viscosity and edge permeability (Crist et al. 1992; With 1994; Wiens et al. 1997; McIntyre 2000). Dispersing spadefoots may have been unable to penetrate geometrically complex agricultural landscapes (Rothermel and Semlitsch 2002), resulting in increased abundance near their natal wetlands, while this may have had little influence on the larger tiger salamanders and Great Plains toads. Several studies have documented increased numbers of spadefoots and other small-bodied amphibians at wetlands embedded in agricultural landscapes (Knutson et al. 1999; Kolozsvary and Swihart 1999; Gray et al. 2004), which are more geometrically complex in the Southern High Plains (Gray 2002). Similarly,

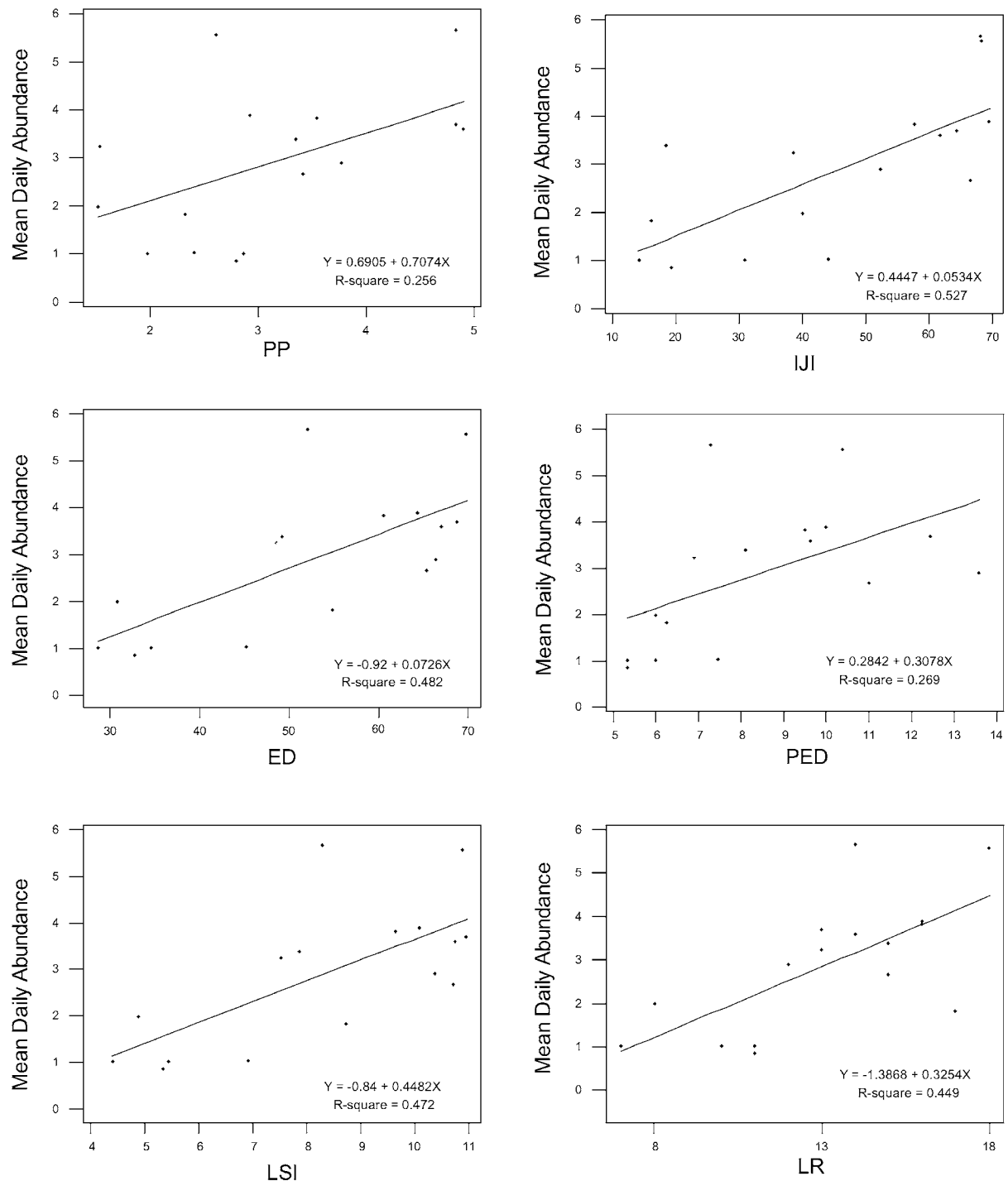


Figure 2. Simple linear regression of relative abundance (natural-log transformed) of New Mexico spadefoot and percent aerial coverage of playa wetlands (PP), interspersion/juxtaposition index (IJI, McGarigal and Marks 1995:103), edge density (ED, McGarigal and Marks 1995:106), playa edge density (PED [i.e., mean number of edges to cross from study playa to surrounding playas]), landscape shape index (LSI, McGarigal and Marks 1995:109), and land-use type richness (LR, McGarigal and Marks 1995:119) in landscapes (i.e., 2,830-ha circular plot) associated with 16 study playas in the Southern High Plains, Texas, 1999 and 2000.

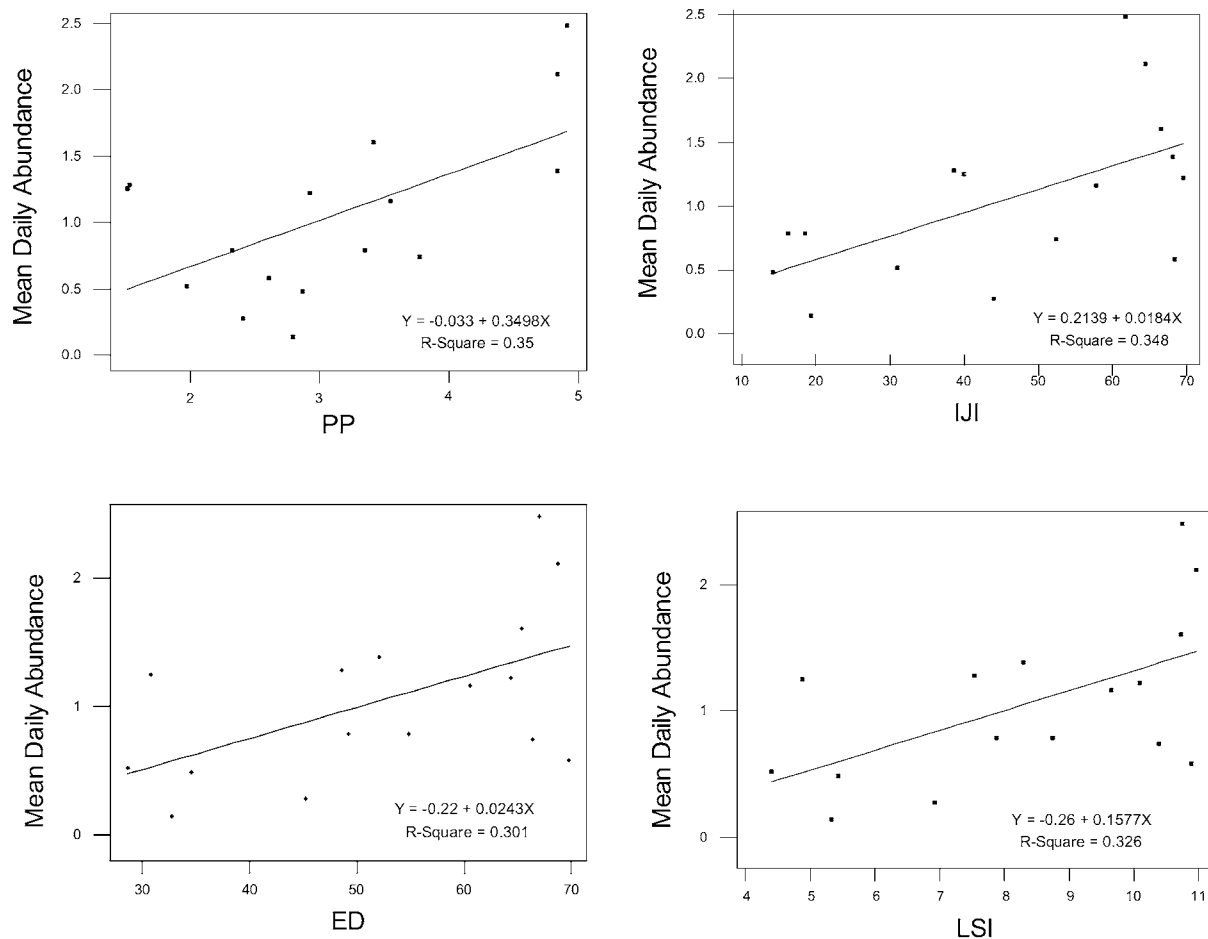


Figure 3. Simple linear regression of relative abundance (natural-log transformed) of plains spadefoot and percent aerial coverage of playa wetlands (PP), interspersion/juxtaposition index (IJI, McGarigal and Marks 1995:103), edge density (ED, McGarigal and Marks 1995:106), and landscape shape index (LSI, McGarigal and Marks 1995:109) in landscapes (i.e., 2,830-ha circular plot) associated with 16 study playas in the Southern High Plains, Texas, 1999 and 2000.

abundance of spadefoots may have been negatively associated with playa isolation, because probability of interdemarc movement and abundance can decrease with increasing inter-patch distance as predicted by island biogeography and metapopulation theories, particularly for less vagile organisms such as amphibians (Bascompte and Solé 1996; Hess 1996; Ritchie 1997; Stacey et al. 1997). The negative association of amphibians with wetland isolation has been documented (Sjögren 1991; Marsh and Pearman 1997; Pope et al. 2000).

Great Plains toad and barred tiger salamander may have been negatively associated with spadefoots because of differential competitive ability of their larvae (Gray et al. 2004). Spadefoot larvae have been shown to outcompete various genera (Morin 1983;

Wilbur 1987; Dayton and Fitzgerald 2001). Postmetamorphic interactions also may exist among our amphibian species as suggested by diet composition studies (Anderson et al. 1999; Smith et al. 2004).

Relative abundance relationships with landscape structure and competitive interactions of amphibians in the Southern High Plains also may interact with playa hydroperiod (Gray et al. 2004). Landscape complexity always was positively associated with increased cultivation in playa watersheds (Gray 2002). Playas with less complex landscapes had watersheds dominated by uncultivated grasslands. Watershed cultivation in complex landscapes increases wetland sedimentation, consequently decreasing playa hydroperiod via reducing playa volume (Luo et al. 1997). Shorter hydroperiod in playas can alter competitive



relationships within the larval amphibian community (Smith 2003). Moreover, amphibian community dynamics, including intra-guild predation, can be altered and amphibian body size negatively influenced by agricultural cultivation (Gray 2002, Smith et al. 2004). Indeed, the relative influence of wetland hydroperiod versus landscape structure on Southern High Plains amphibians is difficult to separate. Controlled studies investigating the relationship of landscape structure, wetland hydroperiod, and amphibian community interactions are needed.

### *Conservation implications*

Agricultural landscape structure influences species composition and relative abundance of playa amphibians but the exact mechanism of that influence is unknown. Increasing geometric complexity in agricultural landscapes may affect certain species (as per body size and perception to landscape permeability) by reducing probability of interdemarc movement, which can have negative demographic and genetic effects (Wiens 1997). Landscape complexity also can affect the wetland through its indirect influence on hydroperiod. Landscape ecologists should consider species-specific mobility and indirect hydroperiod effects when developing conservation initiatives for spatially structured amphibian populations (Driscoll 1997; Szacki 1999). In addition, these results suggest that inter-patch landscape complexity is an important factor affecting intra-patch species responses. This has been suggested by theoretical (e.g., Stamps et al. 1987) and artificially constructed landscape studies for insects (e.g., With 1994). Researchers should consider inter-patch complexity when planning conservation endeavors and estimating dispersal probabilities for metapopulation and other spatially-explicit demographic models.

In the Southern High Plains, landscape planners and ecologists should consider restoration and conservation of native prairie to re-establish or maintain natural landscape structure and inter-playa connectivity. However, planting structurally dense and tall exotic grasses through Conservation Reserve Program in the United States may negatively influence landscape permeability (Smith 2003). Although comparative species-specific vagility studies among native and exotic grass species are needed, we believe grassland restoration efforts should use native short prairie grasses to predictably facilitate interdemarc movement of small-bodied organisms. Following

prairie restoration, sediments can be removed from the playa basin to restore the natural hydroperiod. Hydroperiod restoration likely would permit return of more natural competitive relationships at the larval stage. Presumably, competitive ability interacts synergistically with landscape structure and species-specific vagility thus should be considered in conservation endeavors for amphibians.

Existing spatial software packages (e.g., FRAGSTATS\*ARC®, RAMAS® GIS) have options for inclusion of relative patch viscosity, boundary permeability, and species vagility data; however, generally unity or non-empirical estimates are used because the aforementioned data do not exist. Future research directives should focus on estimation of species-specific vagility in anthropogenic and native cover types and the relative permeability of their boundaries for realistic estimation of extrinsic connectivity among habitat patches (e.g., With and Crist 1995; Wiens et al. 1997; Rothermel and Semlitsch 2002). Estimates of genetic variability among spatially structured populations would further elucidate these relationships (e.g., Scribner et al. 2001). Our regression models presented herein certainly could be used to predict relative abundance of small-bodied amphibian populations in agricultural landscapes given structure indices. Moreover, these baseline amphibian abundance data and linear landscape structure relationships can be used to perform population viability analyses for spatially structured amphibian populations.

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